Estuaries and Coasts
DOI 10.1007/s12237-015-9945-3

Small-Scale Nekton Density and Growth Patterns Across a Saltmarsh Landscape in Barataria Bay, Louisiana

Lawrence P. Rozas · Thomas J. Minello

Received: 25 June 2014 / Revised: 15 December 2014 / Accepted: 19 January 2015

Abstract Nekton on the northern Gulf of Mexico depend on estuarine nursery areas, but patterns of habitat use and the underlying processes that drive these patterns are not fully understood. We examined small-scale (1–50 m) patterns of habitat use in Barataria Bay by collecting nekton samples between 2002 and 2006 with a 1-m^2 drop sampler. Habitat-specific densities were estimated for six habitat types at various distances from the shoreline in marsh (Marsh1M=1 m and Marsh3M=3 m) and over shallow nonvegetated bottom, SNB (SNB1M=1 m, SNB5M=5 m, SNB20M=20 m, and SNB50M=50 m). Habitat-specific growth rates also were estimated for brown shrimp *Farfantepenaeus aztecus* caged in SNB1M, SNB5M, and SNB20M. Nekton density patterns in Barataria Bay appeared to be clearly different from the Galveston Bay model, which predicts nekton distribution patterns relative to the marsh shoreline. Although densities in Barataria Bay were significantly higher in samples near the marsh shoreline (Marsh1M or SNB1M) for brown shrimp, blue crab, and white shrimp, highest mean densities were not always present in marsh edge vegetation. In addition, densities of brown shrimp and white shrimp in Barataria Bay declined much more steeply with distance into the marsh than in the model. Daily growth rates (1.0–1.2 mm TL day^{-1}, 68–89 mg day^{-1}) for brown shrimp were similar among SNB habitat types. Our results suggest that SNB in Barataria Bay may be relatively more important as habitat for fishery species than previously assumed.

Keywords Marsh edge · Fishery habitat · *Spartina* marsh · Growth experiment

Communicated by Alf Norkko

L. P. Rozas (✉)
NOAA/National Marine Fisheries Service/SEFSC, Estuarine Habitats and Coastal Fisheries Center, 646 Cajundome Boulevard, Lafayette, LA 70506, USA
e-mail: Lawrence.Rozas@noaa.gov

T. J. Minello
NOAA/National Marine Fisheries Service/SEFSC, Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551, USA

Introduction

Wetlands and adjacent shoals provide important habitat in estuaries of the northern Gulf of Mexico (Minello 1999), and their use by nekton appears to be hydrologically driven (Rozas 1995; Baker et al. 2013). This habitat supports a nekton community that includes some of the most abundant, and ecologically important, estuarine residents (e.g., killifishes, grass shrimps, gobies) as well as the young of transient fishery species (e.g., white shrimp *Litopenaeus setiferus*, brown shrimp *Farfantepenaeus aztecus*), which spawn offshore or in nearshore waters and use estuaries temporarily as nursery areas.

This nekton community seems to aggregate at the marsh shoreline (edge), an ecological hotspot where biological interactions and nekton densities are high (Baltz et al. 1993; Peterson and Turner 1994; Minello and Rozas 2002; Stunz et al. 2002). When flooded, the marsh edge habitat appears to be selected by a wide variety of nekton species in northern Gulf of Mexico estuaries (Minello 1999), but detailed information on small-scale (1–50 m) distributions in relation to marsh edge is lacking for most species.

A model developed for Galveston Bay predicts that densities of brown shrimp, white shrimp, and blue crab *Callinectes sapidus* peak within marsh vegetation just inside the marsh–water interface (at the vegetated edge) and decline rapidly with distance into the marsh vegetation and from the vegetated marsh edge out over shallow nonvegetated bottom (SNB) or open water (Minello and Rozas 2002; Minello et al. 2008).

Published online: 27 February 2015

Although this flood–tide distributional pattern is often assumed for coastal marshes in general, these small-scale distribution patterns have seldom been examined in other marsh systems to test the generality of this Galveston Bay model. There is some evidence that selection and value of this marsh edge habitat is affected by tidal inundation patterns (Minello et al 2012; Baker et al. 2013).

The value of coastal or estuarine habitats for fishery species can be measured using several metrics (Beck et al. 2001), and density patterns are often used for an initial assessment. Although difficult to estimate directly, habitat-specific vital rates (e.g., growth, survival) are also useful measures of habitat value (Beck et al. 2001; Yoklavich et al. 2010; Mace and Rozas 2015). In addition, vital rates are used in stock assessment models to manage exploited fishery populations, and variation in these rates can have a significant effect on estimates of adult stocks. For example, simulations from a population model incorporating the available information on vital rates showed that even modest changes in growth rates of juvenile white shrimp had a greater effect on stock size than the highest mortality rate expected from fishing (Baker et al. 2014).

The Barataria Bay estuary is part of the Mississippi River deltaic plain, which includes the largest expanse of tidal saltmarsh in the northern Gulf of Mexico. The wetlands of Barataria Bay and other estuaries of this deltaic system support some of the most productive coastal fisheries in North America (Viosca 1928; Gunter 1967; Chesney et al. 2000). Because of its importance in supporting coastal fisheries and the different origin of marshes in Barataria Bay (deltaic, river-dominated) and Galveston Bay (washover fan, barrier island), we selected Barataria Bay to test the generality of the Galveston Bay model for nekton distribution patterns. We also wanted to estimate habitat-specific growth rates for a selected species to complement these density data for within-habitat and across-estuary comparisons.

Acquiring this information is important because Barataria Bay is undergoing rapid change, and nekton growth and distributional data could be used as a baseline against which to measure this change. An understanding of nekton distributional patterns within marsh systems, for example, could be used to predict how landscape changes that alter marsh–water interspersion patterns affect nekton abundance (Minello and Rozas 2002; Reed et al. 2007; Roth et al. 2008). Changes in marsh–water interspersion patterns are currently underway in Barataria Bay from a relatively rapid rate of wetland loss caused by subsiding deltaic sediments and resource extraction (Turner 1997; Day et al. 2000; Roberts 1997) and by a variety of wetland restoration techniques being implemented in response to this loss (CPRA 2012). Both wetlands and nekton populations in the estuary also have been damaged by the Deepwater Horizon oil spill (Whitehead et al. 2011; Mendelssohn et al. 2012; Rozas et al. 2014), and the habitat-specific data reported here (collected before the spill) should be useful for examining spill impacts on living resources.

The primary objective of our study was to examine the small-scale (1– 50 m) patterns of nekton distribution in lower Barataria Bay and test the generality of the Galveston Bay model of habitat-specific nekton densities. Our density data were derived from nekton samples collected between 2002 and 2006 in hydrologically connected emergent marsh vegetation and adjacent SNB located at various distances from the marsh shoreline. In addition, habitat-specific growth rates were measured for juvenile brown shrimp held in field mesocosms placed within a subset of the habitat types we sampled for nekton density.

Methods

Study Area

The study area included three locations within the Barataria Bay system, which is bounded on the west by Bayou Lafourche and on the east by the Mississippi River (Fig. 1). Rakocinski et al. (1992) provide a detailed description of the estuary. We collected all samples and conducted growth experiments within the saline vegetation-salinity zone as defined and mapped by Chabreck (1972) and Linscombe and Chabreck (2001). This saline zone is comparable to the polyhaline zone of the Venice system (Anonymous 1958; Visser et al. 1998). Emergent vegetation was dominated by *Spartina alterniflora*, and sample sites over shallow open water lacked submerged vegetation (they were classified as SNB). Tides in the study area are predominantly diurnal and have a mean daily range of <0.3 m (Byrne et al. 1976; Baumann 1987). The degree of marsh flooding varies seasonally; longest marsh flooding durations occur in fall and spring (Rozas 1995; Minello et al. 2012).

Nekton Density

We sampled nekton within and adjacent to marshes six times over 3 years (2002, 2005, and 2006) by collecting 124 samples each in spring and fall during a week of high tides that flooded the marsh surface (Table 1). We took samples of emergent marsh habitat 1 m (Marsh1M or marsh edge) and 3 m (Marsh3M) from the shoreline, except in 2006 when only marsh edge was sampled. Over SNB, we collected samples at four distances from the marsh shoreline (SNB1M=1 m, SNB5M=5 m, SNB20M=20 m, and SNB50M=50 m), except in 2006 when SNB50M was not sampled. Sample sites were selected using random numbers and aerial photographs of the study area. The distance from shore was determined using a hand held laser range finder for distances of 20 m or more and a meter tape for shorter distances.

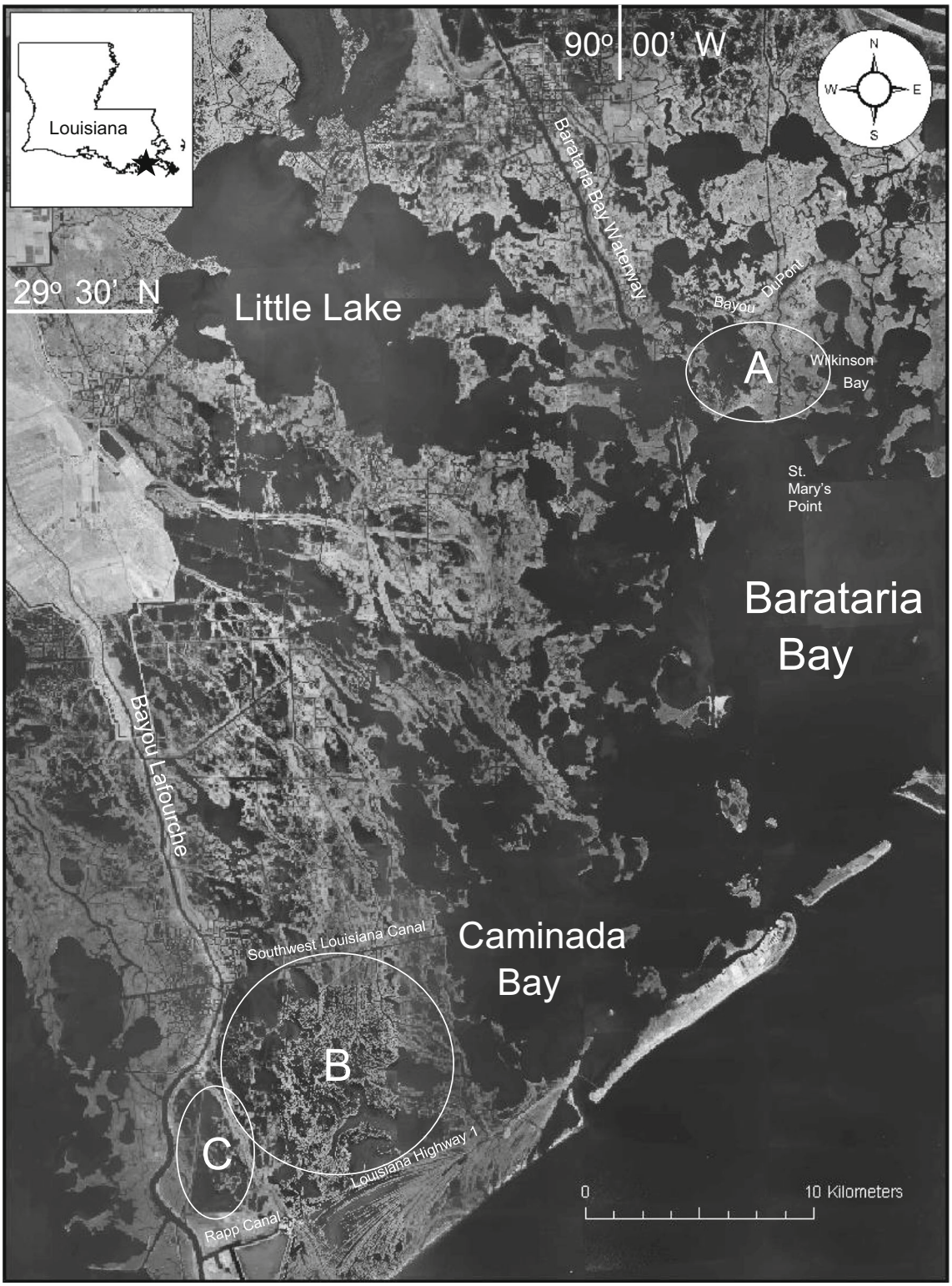

Fig. 1 Map showing three sampling locations within the Barataria Bay estuary study area. *Area A* is south of Bayou DuPont, north of St. Mary's Point, east of Barataria Bay Waterway, and west of Wilkinson Bay. *Area B* is south of Southwest Louisiana Canal, north and east of Louisiana Highway 1, and west of Caminada Bay. *Area C* is south of Southwest Louisiana Canal, north of Rapp Canal, west of Louisiana Highway 1, and east of Bayou Lafourche.

Nekton samples were collected using 1-m^2 drop samplers and the method described by Zimmerman et al. (1984). We used two boats and crews of three persons each to collect these samples. Immediately after the drop sampler was deployed at

Table 1 Description of nekton sampling effort between 2002 and 2006, which included six sampling trips

			Number of samples collected					
			Marsh		SNB			
Sampling dates	Location	Season	3 m	1 m	1 m	5 m	20 m	50 m
April 26–May 2, 2002	A	Spring	4	4	4	4	4	4
September 13–17, 2002	A	Fall	4	4	4	4	4	4
April 26–29, 2005	B	Spring	10	10	10	10	10	10
October 11–13, 2005	B	Fall	10	10	10	10	10	10
April 30–May 3, 2006	C	Spring		10	10	10	10	
October 3, 2006	C	Fall		5	5	5	5	
October 4, 2006	B	Fall		5	5	5	5	
Sum			28	48	48	48	48	28

During each trip, samples were collected within salt marsh and over adjacent shallow nonvegetated bottom (*SNB*) in Barataria Bay. Season, dates of sampling events, and number of samples taken in each habitat type are given for each location shown in Fig. 1. Latitude and longitude indicate approximate center of sample area: location A (29.480° N, 89.955° W), Location B (29.212° N, 90.153° W), and location C (29.180° N, 90.210° W)

a sample site, we measured water temperature, dissolved oxygen (DO), water depth, and distance to marsh edge (from the center of the sampler to the nearest marsh shoreline); collected a water sample from which salinity and turbidity were determined in the laboratory; and removed and counted plant stems (alive and dead combined) at marsh sites as described by Rozas et al. (2012). The spatial location of each nekton sample site was determined using a GPS unit.

After measuring the environmental variables and removing vegetation, we captured nekton trapped in the drop sampler using dip nets and filtering the water pumped out of the enclosure through a 1-mm-mesh net. When the sampler was completely drained, any animals remaining on the bottom were removed by hand. Samples were preserved in formalin and returned to the laboratory for processing.

In the laboratory, the samples were sorted, and animals were identified to lowest feasible taxon. We used the nomenclature of Perez-Farfante and Kensley (1997) for penaeid shrimps and identified species using the protocol described in Rozas and Minello (1998). Forty-six penaeid shrimps could not be reliably identified from the nekton samples either because of their size (total length, 13–18 mm) or because they were damaged; these shrimps were assigned as brown shrimp based on the proportion of identified species in each sample. Grass shrimps (521) that could not be identified to species were similarly assigned as daggerblade grass shrimp *Palaemonetes pugio* (447), marsh grass shrimp *Palaemonetes validus* (45), or brackish grass shrimp *Palaemonetes intermedius* (29). Similarly, 425 swimming crabs of the genus *Callinectes* (425) were considered blue crab *C. sapidus*, and a single specimen of *Brevoortia* spp. was assumed to be a gulf menhaden *Brevoortia patronus*. All individuals within a species were blotted dry and pooled to determine biomass (±0.1 g wet weight).

Growth Experiment

We initiated a growth experiment at location C on April 28, 2006 when juvenile brown shrimp were abundant in the study area (Fig. 1). Shrimp were held in mesocosms, bottomless fiberglass cylinders (1.14 m in diameter, 1.5–1.8 m tall, enclosing 1 m^2 of habitat) with three windows covered in 3-mm mesh. These mesocosms were placed at randomly selected sites in four of the habitat types sampled for nekton density (Marsh1M, SNB1M, SNB5M, and SNB20M), and each habitat treatment was replicated seven times in the experiment (total of 28 mesocosms). The mesocosms were dropped into place from a boom attached to a shallow draft boat (comparable to deployment of a drop sampler), and no attempt was made to remove nekton (potential competitors and predators) from the area before hand. Mesocosms were pushed 15 cm into the sediment to provide a seal intended to hold water at low tide. The bottoms of the mesh windows were located 15 cm above the sediment surface. For a detailed description of these mesocosms and the setup, see Rozas and Minello (2009).

To initiate an experiment, brown shrimp were collected from the study area, measured for total length (TL), and individually marked with a visible implant elastomer (Northwest Marine Technology, Inc.); five individuals were placed into each of the mesocosms. To reduce handling stress, we estimated initial weights of experimental shrimp using length–weight relationships derived from other specimens collected at the beginning of the experiment.

During the experiment, we measured environmental variables that could have affected shrimp growth. We used 12 data loggers (Onset Computer Corp.) to continuously measure bottom water temperature in selected mesocosms during the experiment. Water depth, water temperature, salinity, and DO

were measured at each mesocosm during the day approximately daily (n=6) during the experiment, and the water temperature measured from this daily monitoring was used to assess the reliability of the continuous temperature loggers. Flooding durations for habitats were determined using a temporary tide gauge that continuously recorded water level data throughout the experiment. Combined with water depths measured at each mesocosm, we calculated the extent of flooding outside of each mesocosm over the experimental duration.

The growth experiment was run for ~7 days. At its conclusion, we used dip nets and removed the water from inside the mesocosms with a gasoline-powered centrifugal pump to collect the shrimp and other nekton (Rozas and Minello 2009). Recovered animals were immediately placed on ice, and each tagged shrimp was weighed and measured within 15 h to determine its final size. Because TL could not be measured for shrimp with broken rostrums, we estimated the TL of these shrimp (n=6) based on their final weight from length–weight equations derived as described above for initial lengths. We determined growth rates for each recovered experimental shrimp by subtracting the initial size measurement (TL or wet weight) from the final size measurement and dividing this difference by the duration (in days) of the experiment.

Unmarked fishes and decapod crustaceans collected from the mesocosms when we recovered the marked shrimp may have affected shrimp growth or survival through competition or predation. These organisms were identified to the lowest feasible taxon and measured (TL of fishes, CW=carapace width for crabs). Individuals of each species in a sample were blotted dry and pooled to determine biomass (wet weight).

Statistical Analyses

We analyzed density data for the spring and fall seasons separately. The nekton data were collected in different locations and years, and we were concerned that these differences would influence our analysis of nekton spatial patterns. Therefore, we initially used a two-way analysis of variance (ANOVA) on a subset of our nekton data to explore that possibility and to look for differences in nekton abundance and environmental characteristics among locations/years. In this analysis, we excluded data from Marsh3M and SNB50M sites because these habitat types were not sampled in 2006. This two-way ANOVA included a location/year factor with three (spring) or four (fall) levels (A/2002, B/2005, B/2006, C/2006), a habitat type factor with four levels (Marsh1M, SNB1M, SNB5M, and SNB20M), and an interaction term. A significant interaction term may indicate differences in nekton density patterns across locations/years. Therefore, where significant interactions were detected, we examined plots of the nekton data to help us interpret distribution patterns.

Despite the inclusion of location/year variability, we assumed that the overall dataset would provide a meaningful comparison of habitat use, and we also used a one-way ANOVA on all the density data followed by a priori contrasts to examine density patterns of abundant fishes and decapod crustaceans among habitat types. The density data used in all ANOVAs were transformed [ln(x + 1)] to remove the relationship between the mean and variance present in untransformed data (Milliken and Johnson 1992). When a significant main effect was detected in one-way ANOVAs, the following habitat types were compared with a priori contrasts: (1) Marsh1M vs. Marsh3M, (2) Marsh1M vs. SNB1M, and (3) SNB1M vs. SNB5M+SNB20M+SNB50M. The first two contrasts tested for differences in nekton density between the marsh edge and marsh sites farther (3 m) from shore or over nearshore open water sites. The third contrast examined whether nekton density at SNB sites was related to the proximity of marsh vegetation.

Environmental characteristics (salinity, water temperature, DO, water depth, turbidity, and distance to shoreline) of nekton sample sites were analyzed using untransformed data and the same ANOVA models. Untransformed stem density data were analyzed using a two-way ANOVA that included only two locations/years (location A/2002, location B/2005) and the two marsh habitat types.

Minello et al. (2012) examined salt marsh flooding patterns in estuaries and reported a potential relationship between flooding durations and use of marsh edge habitat by brown shrimp, white shrimp, and blue crabs. Using our nekton data, we looked for such a relationship by developing a simple selection index for these species. The index was computed using habitat-specific means of transformed [ln(x + 1)] densities for each of the seven location/year/season datasets; selection index=Marsh1M−SNB1M. A positive value would indicate selection for marsh vegetation over adjacent nonvegetated bottom. Marsh flooding durations were calculated for comparison using the water depth measured for each marsh edge sample site along with continuously recorded water level data from the NOAA tide gauge at Grand Isle, LA, USA (station ID=8761724). Linear regression was used to examine whether the use of the marsh edge by these species was potentially related to the flooding duration of that habitat type 1 month before we collected our samples.

We also used regression trees to examine the importance of selected variables on densities of brown shrimp, white shrimp, and blue crabs. Trees are constructed from a series of mutually exclusive binary splits that minimize the within-group sum of squares (SS) and maximize the between-groups SS for each level in the tree, and the relative importance of each explanatory variable in the tree decreases with each split (Deáth 2002). In these analyses, we included the response variable of log-transformed density, three categorical explanatory variables (habitat type, season, location/year), and five continuous explanatory variables (salinity, temperature, DO, turbidity, flooding duration of Marsh1M habitat).

We used the one-way ANOVA model described above, but with fewer levels of habitat type, to analyze untransformed data from the growth experiment. Mean growth rates (mm day^{-1} or mg day^{-1}) computed from each mesocosm were considered to be a single observation in our analyses. When the main effect of habitat type was significant at the 0.05 level, we used Tukey's HSD post hoc tests to compare growth rates among the levels of this treatment, which allowed us to compare growth among all possible pairs of habitat levels while controlling for family-wise type I error (Quinn and Keough 2002).

We examined scatter plots and used regression analysis to explore potential relationships between shrimp growth rates and environmental and biological variables. We used regression analysis to look for possible size-related differences in shrimp growth rates. Regression analysis also was used to examine the potential relationship between shrimp growth rates and competitors or predators and the flooding duration of mesocosm sites. We compared shrimp growth rates in biomass with penaeid biomass, crustacean biomass, and total biomass measured from both marked and unmarked animals recovered from the experimental mesocosms. We also compared the number of recovered marked shrimp (survivors) with predator biomass to test for a possible relationship between the survival of experimental shrimp and predation risk.

We considered alpha levels of 0.05 to be significant in all results, but we also assessed significance after adjusting alpha levels for the main effects using the sequential Bonferroni method described by Rice (1989), which buffers against error introduced by making multiple comparisons with the same sample set. All tabular and graphical (except regression tree) data presented in this paper are untransformed means. We conducted these statistical analyses using JMP software (Version 11.1, Cary, NC, USA, 2013).

Results

We identified a total of 16 crustacean species (1,712 individuals, 1.20 kg) and 35 fish species (478 individuals, 0.39 kg) from 124 samples collected in spring (April–May 2002, 2005, and 2006) and 29 crustacean species (3646 individuals, 0.83 kg) and 41 fish species (1120 individuals, 0.52 kg) from 124 samples taken in fall (September–October 2002, 2005, and 2006). Most crustaceans (83 %) collected in spring consisted of daggerblade grass shrimp, brown shrimp, blue crab, brackish grass shrimp, Harris mud crab *Rhithropanopeus harrisii*, purple marsh crab *Sesarma reticulatum*, and squareback marsh crab *Sesarma cinereum*. Daggerblade grass shrimp, blue crab, white shrimp, brown shrimp, marsh grass shrimp, and purple marsh crab also represented 80 % of the crustaceans collected in fall. The most abundant fish species were gulf menhaden, speckled worm eel *Myrophis punctatus*, bay anchovy *Anchoa mitchilli*, and silver perch *Bairdiella chrysoura* in spring (making up 45 % of all fish) and darter goby *Ctenogobius boleosoma*, naked goby *Gobiosoma bosc*, and bay anchovy in fall (66 % of all fish).

Nekton Density

Location/Year Effects

Densities of some species were significantly different among locations/years, but few strong interactions were apparent between habitat type and location/year (Table 2). Brackish grass shrimp in spring was not collected at location A. Brown shrimp in spring was more abundant at locations B and C than location A. In fall, darter goby was most abundant at locations B and C, and naked goby had the highest densities at location A.

The location/year–habitat type interaction was marginally significant for brown shrimp and speckled worm eel in the spring, but P values were >0.05 after the Bonferroni correction (Table 2). Brown shrimp densities in spring were similar between Marsh1M and SNB1M except at location B in 2005 when mean densities were higher in SNB1M than Marsh1M. In fall, this interaction was highly significant for brown shrimp and blue crab (Table 2), and the distribution of these species among habitat types changed with location/year (Fig. 2). Densities of brown shrimp in fall were higher in Marsh1M than SNB1M except at location B where their densities were similar in these habitat types. Blue crab densities in fall differed among habitat types except at location C in 2006. Bay anchovy was never collected at Marsh1M sites, but few individuals of this species were collected over SNB at Location B in 2005 (Table 2). Speckled worm eel also was more abundant over SNB than at Marsh1M sites, but was not collected at location A in 2002 (Table 2).

Overall Habitat-Related Distribution Patterns

Density patterns for most species of nekton varied across the saltmarsh landscape when we included all habitat types and locations in our analyses (Table 3, Figs. 3 and 4). Within the marsh vegetation, most abundant crustaceans were concentrated at the marsh edge (Marsh1M). Daggerblade grass shrimp, brown shrimp, blue crab (spring), brackish grass shrimp (spring), white shrimp (fall), and marsh grass shrimp (fall) were more abundant at marsh edge than Marsh3M sites. Harris mud crab was not collected at Marsh3M sites. In contrast, our analysis detected no differences between the two marsh habitat types in mean densities of blue crab, darter goby, and naked goby in fall.

Several species also were more abundant at marsh edge (Marsh1M) than nearshore SNB (SNB1M) sites (Table 3, Figs. 3 and 4). Mean densities of daggerblade grass shrimp, blue crab (spring), brackish grass shrimp (spring), and brown

Table 2 Comparison of mean m^{-2} (SE) densities of decapod crustaceans and fishes collected within marsh and over adjacent shallow nonvegetated bottom (SNB) during different sampling events between 2002 and 2006

	Location/year										Habitat type											
	A 2002		B 2005		B 2006		C 2006		ANOVA		MARSH1M		SNB1M		SNB5M		SNB20M		ANOVA	MARSH1M	SNB1M vs.	Interaction
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P* value		Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P* value	vs. SNB1M	SNB 5M 20M	*P* value
Spring																						
Crustaceans	12.0	(3.11)	13.1	(2.02)			18.4	(3.77)	0.5617		33.3	(5.21)	15.5	(2.14)	8.7	(1.59)	2.9	(0.71)	0.0001[a]	0.0004	0.0003	0.1818
Daggerblade grass shrimp	2.3	(1.33)	3.0	(1.14)			6.4	(2.60)	0.2335		14.7	(4.14)	1.1	(0.39)	1.2	(0.74)	0.2	(0.13)	0.0001[a]	0.0000	0.3880	0.8881
Brown shrimp	2.4	(0.66) a	6.1	(1.05) b			7.2	(1.11) b	0.0045[a]		6.6	(1.34)	10.7	(1.64)	4.6	(0.87)	1.8	(0.46)	0.0004[a]	0.2518	0.0013	0.0420
Blue crab	0.9	(0.24)	1.7	(0.39)			1.3	(0.31)	0.3705		3.4	(0.56)	0.9	(0.20)	1.1	(0.37)	0.1	(0.07)	0.0001[a]	0.0001	0.0739	0.7517
Brackish grass shrimp	0.0	(0.00) a	0.4	(0.40) a			1.1	(0.43) b	0.0159		1.8	(0.75)	0.6	(0.58)	0.0	(0.04)	0.1	(0.13)	0.0514			0.4067
Harris mud crab	0.9	(0.27) a	0.8	(0.40) ab			0.2	(0.07) b	0.0312		0.1	(0.06)	0.6	(0.22)	1.3	(0.63)	0.3	(0.19)	0.0140	0.0235	0.9853	0.2544
Fishes	3.5	(0.89)	2.6	(0.48)			6.2	(1.65)	0.3072		4.0	(1.75)	5.1	(1.58)	6.6	(1.71)	1.3	(0.26)	0.0182	0.2907	0.2255	0.2249
Silver perch	0.0	(0.00)	0.0	(0.00)			0.9	(0.82)	0.1459		1.4	(1.37)	0.1	(0.06)	0.0	(0.04)	0.0	(0.00)	0.6704			0.6653
Speckled worm eel	0.0	(0.00) a	0.9	(0.28) b			0.3	(0.10) a	0.0027[a]		0.0	(0.04)	0.5	(0.16)	1.2	(0.45)	0.2	(0.08)	0.0191	0.1158	0.8249	0.0200
Gulf menhaden	0.5	(0.50)	0.0	(0.00)			1.7	(0.92)	0.1109		0.0	(0.04)	2.0	(1.16)	1.2	(1.08)	0.0	(0.00)	0.1517			0.5766
Bay anchovy	0.6	(0.29)	0.1	(0.04)			0.7	(0.49)	0.1226		0.0	(0.00)	0.3	(0.19)	1.2	(0.81)	0.1	(0.09)	0.1524			0.0465
Fall																						
Crustaceans	28.6	(8.21)	23.5	(5.53)	32.2	(9.66)	46.6	(11.99)	0.1115		73.7	(11.79)	25.3	(3.91)	14.5	(4.76)	10.3	(2.01)	0.0001[a]	0.0002	0.0151	0.0094
Daggerblade grass shrimp	9.5	(5.80)	6.2	(3.31)	11.7	(6.46)	10.9	(6.36)	0.3910		33.7	(8.18)	1.5	(0.61)	0.1	(0.09)	0.1	(0.07)	0.0001[a]	0.0000	0.1156	0.4332
Blue crab	8.9	(1.64)	8.2	(1.73)	8.2	(1.82)	12.0	(3.47)	0.2467		11.2	(1.68)	11.6	(2.49)	8.9	(2.94)	4.7	(1.29)	0.0110	0.5711	0.0814	0.0001[a]
White shrimp	5.1	(2.79) ab	1.7	(0.47) b	2.4	(1.15) b	12.7	(4.35) a	0.0061[a]		10.8	(3.59)	5.8	(2.13)	1.1	(0.66)	0.9	(0.59)	0.0001[a]	0.0952	0.0030	0.2892
Brown shrimp	1.1	(0.52)	1.5	(0.51)	0.8	(0.25)	3.5	(1.57)	0.1269		3.2	(0.89)	1.0	(0.37)	2.0	(1.25)	0.5	(0.28)	0.0064[a]	0.0056	0.7808	0.0031[a]
Marsh grass shrimp	0.6	(0.56)	1.3	(0.69)	0.3	(0.20)	1.8	(1.09)	0.4729		2.7	(1.19)	1.5	(0.88)	0.0	(0.04)	0.1	(0.06)	0.0429	0.2888	0.1142	0.7498
Fishes	25.1	(6.03) a	6.7	(1.06) b	8.9	(1.66) ab	6.9	(2.06) b	0.0035[a]		14.0	(3.88)	10.3	(2.27)	11.1	(3.01)	5.6	(0.79)	0.1755			0.0926
Darter goby	1.6	(1.38) a	3.3	(0.64) b	3.5	(0.93) b	3.0	(0.88) b	0.0136		5.0	(1.20)	3.1	(0.79)	2.3	(0.82)	1.4	(0.35)	0.0986			0.3089
Naked goby	12.4	(3.14) a	0.5	(0.14) b	0.9	(0.56) b	1.3	(0.86) b	0.0001[a]		3.5	(1.79)	4.0	(1.80)	2.8	(1.23)	0.5	(0.24)	0.0059[a]	0.4924	0.0162	0.1736
Bay anchovy	2.6	(1.70)	0.6	(0.42)	2.2	(1.06)	1.1	(0.58)	0.1288		0.0	(0.00)	1.8	(0.97)	2.8	(1.27)	1.0	(0.39)	0.0254	0.0389	0.5920	0.3147

Means for each location/year were estimated from 16, 40, and 40 samples for A 2002, B 2005, and C 2006, respectively, in spring and from 16, 40, 20, and 20 samples for A 2002, B 2005, B 2006, and C 2006, respectively in fall. Means for each habitat type were estimated from 24 samples. Data from MARSH3M and SNB1M sites (not shown) were excluded from two-way ANOVAs. ANOVA results (*P* values) are given for comparisons of mean densities among locations/years and habitat types. The total and residual degrees of freedom in the ANOVA model were 95 and 84, respectively, in spring and 95 and 80, respectively in fall. Means with the same letter cannot be statistically distinguished based on Tukey's HSD post hoc tests

[a] Probability value was significant after alpha was adjusted as described by Rice (1989)

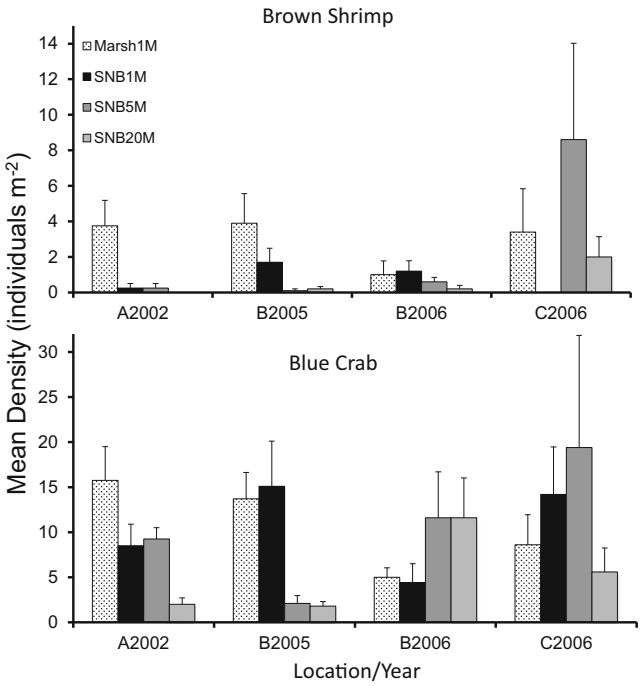

Fig. 2 Fall distributions of brown shrimp (*top panel*) and blue crabs (*bottom panel*) across locations (A, B, and C) and years (2002, 2005, and 2006) within habitat types (Marsh1M, SNB1M, SNB5M, and SNB20M). For each habitat type, means (SEs) were computed from four samples at location A, ten samples at location B in 2005, and five samples each at locations B and C in 2006

shrimp (fall) were higher at marsh edge than SNB1M sites. In addition, purple marsh crab and squareback marsh crab were collected exclusively at marsh sites in spring (Fig. 3).

In contrast to this pattern, during spring when these species were most abundant in the study area, densities of brown shrimp, Harris mud crab, and speckled worm eel were higher at nearshore SNB than marsh edge sites (Table 3, Figs. 3 and 4). In fall, no difference in mean densities of blue crab, white shrimp, and marsh grass shrimp were detected between marsh edge and SNB1M sites. Interestingly, distributional patterns for blue crab and brown shrimp changed seasonally. For example, blue crab appeared to select for marsh edge in spring, but when this species was more abundant in the fall, mean densities were evenly distributed among marsh habitat types and the two SNB habitat types nearest shore. Brown shrimp seemed to select marsh edge in fall, but not in spring.

Within SNB, several species typically associated with marsh vegetation were concentrated at nearshore (SNB1M) sites (Table 3, Figs. 3 and 4). For example, blue crab was more abundant at SNB1M sites than at SNB sites farther from shore. Brown shrimp in spring, and white shrimp, marsh grass shrimp, and naked goby in fall all showed a similar pattern.

Although most species collected in our study occurred in marsh habitat, a few were rarely or never taken from marsh sites (Figs. 3 and 4). For example, bay anchovy was collected exclusively from SNB sites, and speckled worm eel and gulf menhaden were rarely collected at marsh sites.

Environmental Characteristics

Environmental variables also differed among locations/years (Table 4), but within locations/years, few differences among habitat types were detected. Mean salinity was lower at location A than locations B and C. Mean water temperature was lower and turbidity higher at location B than locations A and C. In the spring, DO was higher at location B than locations A and C. No significant location/year by habitat type interaction was detected in these analyses (Table 4). Mean (±SE) stem density was higher at location A (spring=552±112.1, fall=582±119.5) than location B (spring=257±14.6, fall=209±30.3). In spring, stem density did not differ between Marsh1M and Marsh3M. Stem density in fall was higher at Marsh3M, but only at location A. Environmental characteristics (other than water depth and distance to marsh edge) within a location/year did not differ significantly among habitat types (Table 4). When the data were combined across locations/years, however, mean DO differed among habitat types in spring (Table 5). As expected, marsh sites were shallower than SNB sites, and SNB sites generally increased in water depth with distance from the marsh.

Use of the marsh edge increased with flooding duration for brown shrimp and white shrimp. The significant positive relationship (P=0.0013) between our marsh selection index and the flooding duration of the marsh edge 1 month before we collected our samples explained about 70 % of the variability in the data (Fig. 5). There was no significant relationship with flooding for blue crab (P=0.18). Because of a strong (R^2=97 %, P<0.001) negative relationship between our flooding variable and overall (both habitats) mean DO at the time of sampling, marsh selection by shrimp also was significantly related to DO (Fig. 5). These data suggest that, at low levels of DO, shrimp selected for marsh vegetation over adjacent nonvegetated bottom. This selection pattern did not appear to be related to the difference in DO between these two habitats, and there was no significant relationship between marsh selection and the difference in DO between the habitats (P=0.84). Dissolved oxygen was generally higher at SNB1M than Marsh1M (Table 4), but the greatest difference in mean values was only 1.1 mg l^{-1}. All of the mean oxygen levels in these habitats were above 4 mg l^{-1}.

Regression Trees

The results of the regression tree analyses reinforced the ANOVA results. Flooding duration of Marsh1M sites and habitat type were the most important variables explaining the distribution of brown shrimp, white shrimp, and blue crab in the models (Figs. 6, 7, and 8). Flooding duration was driven mainly by season; all flooding durations ≥75 % occurred in fall and ≤66 % occurred in spring. In spring (lower flooding

Table 3 Comparison of mean m^{-2} (SE) densities of decapod crustaceans and fishes collected within marsh and over adjacent shallow nonvegetated bottom (SNB) during three sampling events each in spring and fall between 2002 and 2006

	MARSH				Shallow nonvegetated bottom (SNB)									MARSH1M	MARSH1M	SNB1M
	MARSH3M		MARSH1M		SNB1M		SNB5M		SNB20M		SNB50M		ANOVA	vs.	vs.	vs.
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P* value	MARSH3M	SNB1M	SNB 5M 20M 50M
Spring																
Crustaceans	16.0	(3.77)	33.3	(5.21)	15.5	(2.14)	8.7	(1.59)	2.9	(0.71)	2.9	(0.38)	0.0001[a]	0.0034	0.0020	0.0000
Daggerblade grass shrimp	4.9	(1.28)	14.7	(4.14)	1.1	(0.39)	1.2	(0.74)	0.2	(0.13)	0.0	(0.00)	0.0001[a]	0.0101	0.0000	0.0933
Brown shrimp	0.6	(0.23)	6.6	(1.34)	10.7	(1.64)	4.6	(0.87)	1.8	(0.46)	1.9	(0.33)	0.0001[a]	0.0000	0.0462	0.0000
Blue crab	1.5	(0.77)	3.4	(0.56)	0.9	(0.20)	1.1	(0.37)	0.1	(0.07)	0.1	(0.10)	0.0001[a]	0.0000	0.0000	0.0233
Brackish grass shrimp	0.0	(0.00)	1.8	(0.75)	0.6	(0.58)	0.0	(0.04)	0.1	(0.13)	0.0	(0.00)	0.0012[a]	0.0010	0.0041	0.3352
Harris mud crab	0.0	(0.00)	0.1	(0.06)	0.6	(0.22)	1.3	(0.63)	0.3	(0.19)	0.2	(0.15)	0.0077[a]	0.6970	0.0225	0.2945
Fishes	3.1	(1.22)	4.0	(1.75)	5.1	(1.58)	6.6	(1.71)	1.3	(0.26)	1.9	(0.37)	0.0040[a]	0.6524	0.3576	0.1514
Silver perch	0.0	(0.00)	1.4	(1.37)	0.1	(0.06)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.4762			
Speckled worm eel	0.0	(0.00)	0.0	(0.04)	0.5	(0.16)	1.2	(0.45)	0.2	(0.08)	0.4	(0.23)	0.0010[a]	0.8347	0.0386	0.9499
Gulf menhaden	0.0	(0.00)	0.0	(0.04)	2.0	(1.16)	1.2	(1.08)	0.0	(0.00)	0.0	(0.00)	0.1552			
Bay anchovy	0.0	(0.00)	0.0	(0.00)	0.3	(0.19)	1.2	(0.80)	0.1	(0.09)	0.3	(0.16)	0.2003			
Fall																
Crustaceans	39.8	(10.32)	73.7	(11.79)	25.3	(3.91)	14.5	(4.76)	10.3	(2.01)	8.3	(5.18)	0.0001[a]	0.0469	0.0017	0.0002
Daggerblade grass shrimp	8.4	(3.08)	33.7	(8.18)	1.5	(0.61)	0.1	(0.09)	0.1	(0.07)	3.1	(3.00)	0.0001[a]	0.0003	0.0000	0.1350
Blue crab	10.8	(3.38)	11.2	(1.68)	11.6	(2.49)	8.9	(2.94)	4.7	(1.29)	2.6	(1.16)	0.0004[a]	0.1888	0.6865	0.0008
White shrimp	0.9	(0.40)	10.8	(3.59)	5.8	(2.13)	1.1	(0.66)	0.9	(0.59)	0.9	(0.64)	0.0001[a]	0.0007	0.1128	0.0016
Brown shrimp	0.5	(0.25)	3.2	(0.89)	1.0	(0.37)	2.0	(1.25)	0.5	(0.28)	0.3	(0.22)	0.0025[a]	0.0030	0.0092	0.3611
Marsh grass shrimp	0.4	(0.25)	2.7	(1.19)	1.5	(0.88)	0.0	(0.04)	0.1	(0.06)	0.0	(0.00)	0.0064[a]	0.0368	0.1674	0.0248
Fishes	6.9	(1.80)	14.0	(3.88)	10.3	(2.27)	11.1	(3.01)	5.6	(0.79)	2.9	(0.50)	0.1022			
Darter goby	2.9	(1.09)	5.0	(1.20)	3.1	(0.79)	2.3	(0.82)	1.4	(0.35)	1.0	(0.35)	0.0422	0.1435	0.2129	0.0693
Naked goby	0.4	(0.29)	3.5	(1.79)	4.0	(1.80)	2.8	(1.23)	0.5	(0.24)	0.2	(0.16)	0.0342	0.0571	0.6872	0.0169
Bay anchovy	0.0	(0.00)	0.0	(0.00)	1.8	(0.97)	2.8	(1.27)	1.0	(0.39)	0.1	(0.07)	0.0152	1.0000	0.0277	0.5615

Each mean for MARSH3M and SNB50M is estimated from 14 samples, and other means are estimated from 24 samples. ANOVA results (*P* values) also are given for comparisons of mean densities among habitat types. The total and residual degrees of freedom in the ANOVA model were 123 and 118, respectively

[a] Probability value was significant after alpha was adjusted as described by Rice (1989)

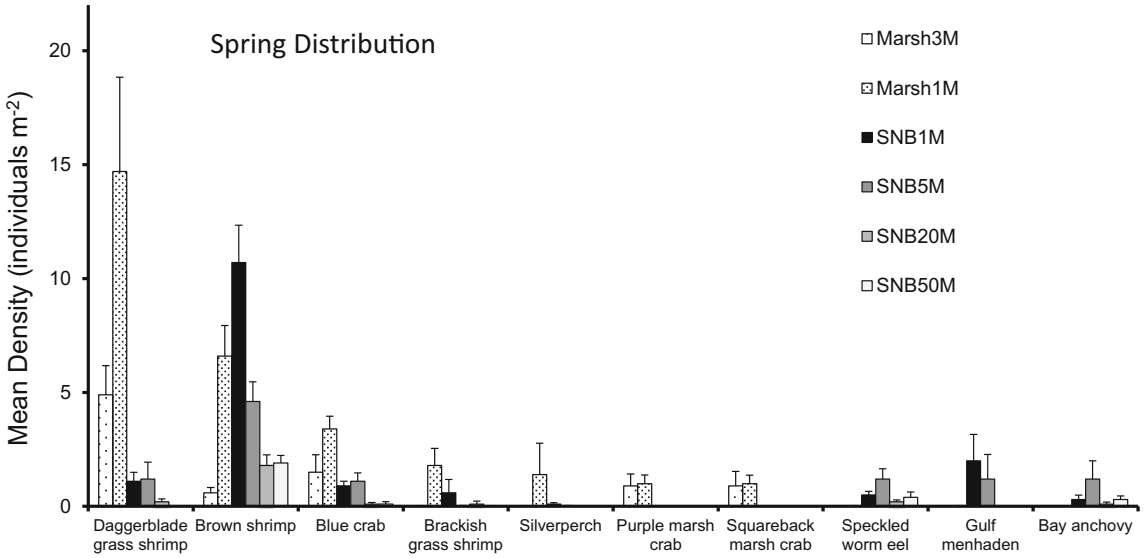

Fig. 3 Comparison of nekton assemblages in marsh (Marsh1M and Marsh3M) and over adjacent shallow nonvegetated bottom (SNB1M, SNB5M, SNB20M, and SNB50M) derived from samples collected in spring. Means (SEs) were computed from 14 samples for Marsh3M and SNB50m and from 24 samples for other habitat types

duration), brown shrimp densities were highest in the habitat types along the marsh shoreline (Marsh1M, SNB1M, and SNB5M), and in fall, densities were highest in Marsh1M (Fig. 6). The structure of the blue crab model was similar, although higher blue crab densities occurred in fall rather than spring; densities in fall were highest in marsh vegetation and SNB located near the marsh, whereas in spring, blue crabs were most abundant in Marsh1M (Fig. 8). White shrimp was collected only during fall when highest densities were in SNB1M and Marsh1M (Fig. 7). A third split in the white shrimp model shows that highest shrimp densities occurred at location C in 2006.

Growth Experiment

Brown shrimp used in the growth experiment ranged in size from 33 to 61 mm TL (mean=47.7±0.713 SE), which reflected the size of juvenile shrimp most abundant in the

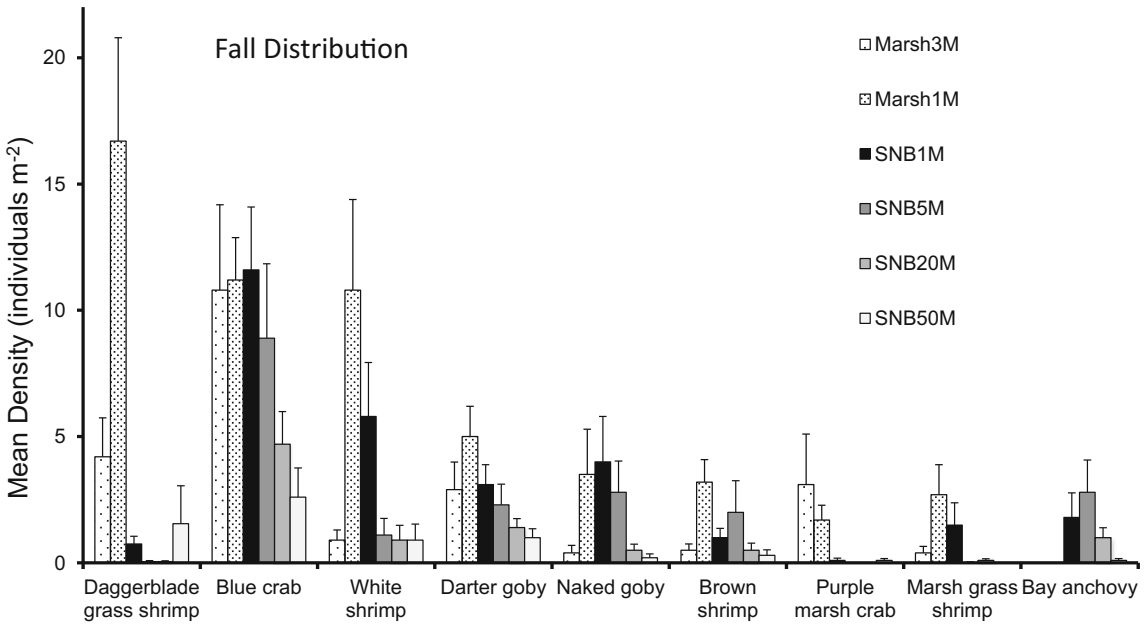

Fig. 4 Comparison of nekton assemblages in marsh (Marsh1M and Marsh3M) and over adjacent shallow nonvegetated bottom (SNB1M, SNB5M, SNB20M, and SNB50M) derived from samples collected in fall. Means (SEs) were computed from 14 samples for Marsh3M and SNB50m and from 24 samples for other habitat types. The data provided for daggerblade grass shrimp represent only 50 % of actual values

Table 4 Comparison of environmental characteristics among locations/years and habitat types

	Location/year												Habitat type										
	A 2002			B 2005			B 2006			C 2006			ANOVA	MARSH1M		SNB1M		SNB5M		SNB20M		ANOVA	MARSH1M	SNB1M vs.	Interaction
Species	Mean	SE		Mean	SE		Mean	SE		Mean	SE		*P* value	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P* value	vs. SNB1M	SNB 5M 20M	*P* value
Spring																									
Water temperature (°C)	28.2	(0.38)	a	24.8	(0.30)	b				27.8	(0.16)	a	0.0001[a]	26.4	(0.54)	26.6	(0.42)	26.8	(0.38)	26.6	(0.43)	0.7496			0.6201
Salinity	7.0	(0.49)	a	22.2	(0.29)	b				24.7	(0.12)	c	0.0001[a]	20.8	(1.45)	21.2	(1.32)	20.4	(1.37)	20.5	(1.25)	0.2763			0.5000
Water depth (cm)	53.8	(5.85)	a	47.9	(4.51)	a				62.7	(3.96)	b	0.0001[a]	18.6	(1.93)	53.1	(2.50)	67.1	(3.46)	81.3	(2.90)	0.0001[a]	0.0000	0.0000	0.6657
Dissolved oxygen (mg l^{-1})	6.2	(0.23)	a	7.2	(0.20)	b				6.6	(0.15)	a	0.0018[a]	6.7	(0.23)	7.3	(0.31)	6.7	(0.18)	6.3	(0.16)	0.1392			0.1225
Turbidity (FTU)	14.0	(2.05)	a	217.6	(28.00)	b				8.6	(0.91)	a	0.0001[a]	106.7	(41.72)	42.8	(9.76)	111.0	(28.00)	121.2	(35.51)	0.2250			0.0677
Distance to marsh edge (m)	6.6	(1.94)		6.9	(1.29)					7.2	(1.28)		0.0957	1.0	(0.04)	1.3	(0.10)	5.4	(0.23)	20.3	(0.37)	0.0001[a]	0.3006	0.0000	0.5289
Fall																									
Water temperature (°C)	30.5	(0.32)	a	26.6	(0.21)	b	28.3	(0.17)	c	28.3	(0.16)	c	0.0001[a]	28.1	(0.36)	27.9	(0.35)	28.0	(0.36)	27.8	(0.39)	0.9707			0.6154
Salinity	11.8	(0.33)	a	24.3	(0.17)	b	25.6	(0.54)	c	26.6	(0.49)	c	0.0001[a]	23.2	(1.16)	22.9	(1.08)	23.0	(1.15)	22.7	(1.05)	0.4697			0.1400
Water depth (cm)	58.2	(7.34)	a	48.7	(3.92)	b	62.6	(7.49)	a	54.3	(5.07)	ab	0.0001[a]	18.8	(0.98)	48.5	(2.37)	66.1	(3.05)	83.9	(3.44)	0.0001[a]	0.0000	0.0000	0.0388
Dissolved oxygen (mg l^{-1})	4.4	(0.40)	a	4.8	(0.14)	ab	5.4	(0.25)	b	4.7	(0.24)	ab	0.0499	4.6	(0.25)	5.0	(0.26)	4.8	(0.22)	5.0	(0.22)	0.6565			0.5349
Turbidity (FTU)	15.4	(8.40)	a	86.1	(11.43)	b	35.6	(4.25)	a	37.5	(7.10)	a	0.0001[a]	63.1	(12.39)	28.6	(5.82)	64.0	(15.15)	58.9	(11.52)	0.3351			0.2222
Distance to marsh edge (m)	6.6	(1.88)	ab	6.6	(1.22)	ab	6.8	(1.87)	a	5.9	(1.48)	b	0.0381	1.0	(0.05)	1.0	(0.06)	5.2	(0.19)	18.9	(0.44)	0.0001[a]	0.7647	0.0000	0.0006[a]

Means and (SE) are given for variables measured within marsh and over adjacent shallow nonvegetated bottom (SNB) during different sampling events between 2002 and 2006. Location/year means were estimated from 16, 40, and 40 samples for A 2002, B 2005, and C 2006, respectively, in spring and 16, 40, 20, and 20 samples for A 2002, B 2005, B 2006, and C 2006, respectively, in fall. Means for habitat types were estimated from 24 samples (except means of turbidity and salinity for MARSH1M in spring were computed from 23 samples). Data from MARSH3M and SNB50M sites (not shown) were excluded from the two-way ANOVA analyses. ANOVA results (*P* values) are given for comparisons of means among locations/years and habitat types. The total and residual degrees of freedom in the ANOVA models were 95 and 84, respectively, in spring and 95 and 80, respectively, in fall. Means with the same letter cannot be statistically distinguished based on Tukey's HSD post hoc tests

[a] Probability value was significant after alpha was adjusted as described by Rice (1989)

Table 5 Comparison of environmental characteristics among habitat categories

Variable	MARSH				Shallow nonvegetated bottom (SNB)									MARSH1M	MARSH1M	SNB1Mnt
	MARSH3M		MARSH1M		SNB1M		SNB5M		SNB20M		SNB50M		ANOVA	vs.	vs.	vs.
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P* value	MARSH3M	SNB1M	SNB 5M 20M 50M
Spring																
Water temperature (°C)	25.1	(0.73)	26.4	(0.54)	26.6	(0.42)	26.8	(0.38)	26.6	(0.43)	25.8	(0.68)	0.2754			
Salinity	17.5	(2.05)	20.8	(1.45)	21.2	(1.32)	20.4	(1.37)	20.5	(1.25)	18.3	(2.11)	0.5553			
Water depth (cm)	13.2	(1.61)	18.6	(1.93)	53.1	(2.50)	67.1	(3.46)	81.3	(2.90)	97.2	(6.50)	0.0001[a]	0.2770	0.0000	0.0000
Dissolved oxygen (mg l^{-1})	6.1	(0.22)	6.7	(0.23)	7.3	(0.31)	6.7	(0.18)	6.3	(0.16)	6.6	(0.23)	0.0180	0.0853	0.0690	0.0059
Turbidity (FTU)	136	(51.8)	107	(41.7)	43	(9.8)	111	(28.0)	121	(35.5)	213	(44.7)	0.0645			
Distance to marsh edge (m)	3.2	(0.10)	1.0	(0.04)	1.3	(0.10)	5.4	(0.23)	20.3	(0.37)	49.9	(0.92)	0.0001[a]	0.0000	0.4155	0.0000
Stem density (stems m^{-2})	313	(45.2)	303	(45.8)	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)				
Fall																
Water temperature (°C)	27.3	(0.68)	28.1	(0.36)	27.9	(0.35)	28.0	(0.36)	27.8	(0.39)	27.2	(0.61)	0.6443			
Salinity	20.7	(1.51)	23.2	(1.16)	22.9	(1.08)	23.0	(1.15)	22.7	(1.05)	21.3	(1.62)	0.7256			
Water depth (cm)	10.6	(1.61)	18.8	(0.98)	48.5	(2.37)	66.1	(3.05)	83.9	(3.44)	86.4	(6.12)	0.0001[a]	0.0810	0.0000	0.0000
Dissolved oxygen (mg l^{-1})	4.3	(0.48)	4.6	(0.25)	5.0	(0.26)	4.8	(0.22)	5.0	(0.22)	4.8	(0.22)	0.5524			
Turbidity (FTU)	27	(5.2)	63	(12.4)	29	(5.8)	64	(15.2)	59	(11.5)	50	(10.8)	0.0742			
Distance to marsh edge (m)	3.1	(0.07)	1.0	(0.05)	1.0	(0.06)	5.2	(0.19)	18.9	(0.44)	49.1	(0.58)	0.0001[a]	0.0000	0.8914	0.0000
Stem density (stems m^{-2})	377	(90.1)	270	(27.4)	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)				

Means and (SE) are given for variables measured within marsh and over adjacent shallow nonvegetated bottom (SNB) during three sampling events each in spring and fall between 2002 and 2006. Each mean for MARSH3M and SNB50M is estimated from 14 samples, and other means are estimated from 24 samples (except in spring, means of turbidity and salinity for MARSH1M were computed from 23 samples). ANOVA results (*P* values) also are given for comparisons of means among habitat types. The total and residual degrees of freedom in the ANOVA model were 123 and 118, respectively

[a] Probability value was significant after alpha was adjusted as described by Rice (1989)

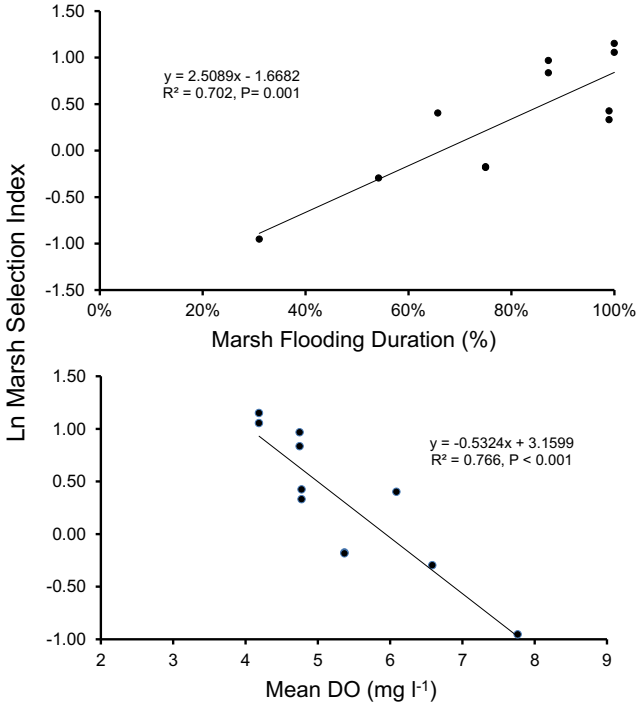

Fig. 5 Selection for marsh by brown and white shrimps in relation to marsh flooding (*above*) and dissolved oxygen (*below*). The selection index is the difference in mean densities (after ln (x+1) transformation of raw data) between Marsh1M and SNB1M; positive values indicate marsh selection. Flooding duration (percent of time marsh surface was available to nekton) was estimated for 1 month before the marsh was sampled. Dissolved oxygen is the mean value for both habitats at the time of sampling

study area. The mean initial size of these experimental shrimp did not differ among habitat types (ANOVA: MS=0.410, $F_{2,104}$=0.008, p=0.993). Initial size affected growth rates, but this relationship between growth and initial size was weak (R^2s<0.10).

During the growth experiment, water levels sometimes fell below the elevation of some mesocosm sites (Fig. 9). The mesocosms were designed to hold water during low water events (Rozas and Minello 2009), but apparently, some mesocosms drained during the experiment. Low tide events generally occurred in the middle of the night when we were not able to observe water levels inside mesocosms. Data from our temporary tide gauge showed that, during the experiment, water levels in the study area were at or below the elevation of the Marsh1M mesocosm sites for periods of up to ten continuous hours. We recovered no marked shrimp from four of the seven marsh mesocosms and no unmarked nekton from five of these mesocosms, an indication that these mesocosms likely failed to hold water. At the end of the experiment, we observed numerous animal burrows through which water inside the mesocosms may have drained out during extended periods of low water. Data from these marsh mesocosms, therefore, were considered unreliable and not included in any analyses. Although low water events had less of an effect in the other habitat types, water levels were at or below the elevation of all SNB1M mesocosm sites for periods of three to five continuous hours.

Water temperature was successfully measured continuously inside and outside at least one mesocosm in each habitat type. These continuously recorded temperature data appeared to match the data we collected through daily monitoring and therefore were considered reliable. Based on these continuously recorded data, the range (mean±SE) of water temperatures during the experiment for SNB1M, SNB5M, and SNB20M were 20.3–29.9 °C (25.2±0.19), 20.5–29.7 °C (25.7±0.17), and 20.7–29.3 °C (26.0±0.15), respectively. Water temperatures measured inside the mesocosms closely tracked outside temperatures.

Salinity and DO were measured inside each mesocosm on 6 days during the experiment. Based on these daily observations,

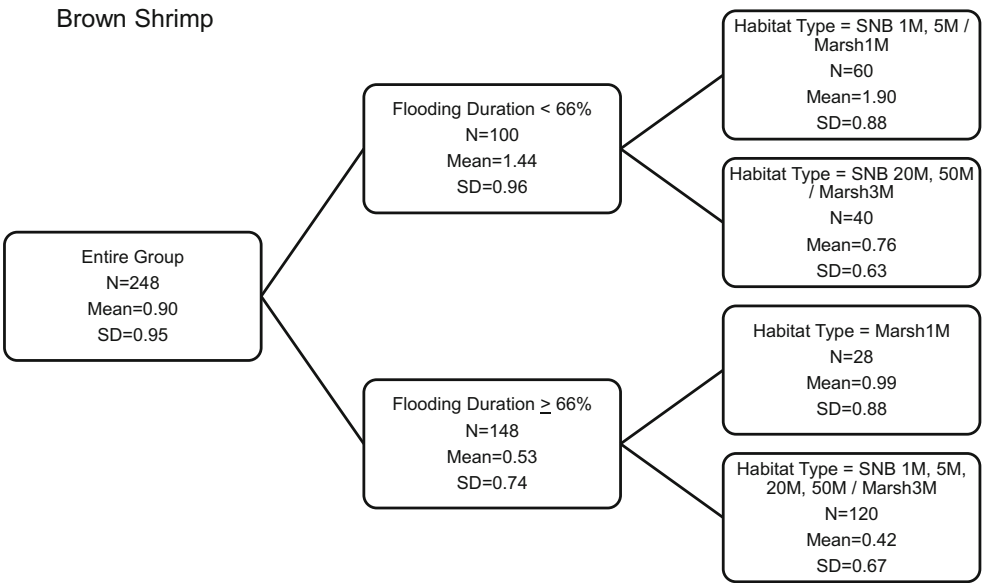

Fig. 6 Regression tree showing distribution of brown shrimp in the study area. Each split in the tree includes the name of the explanatory variable, number of cases (*N*), mean log transformed density (number per square meter), and the standard deviation (*SD*). The cumulative R^2 for the whole model is 0.40

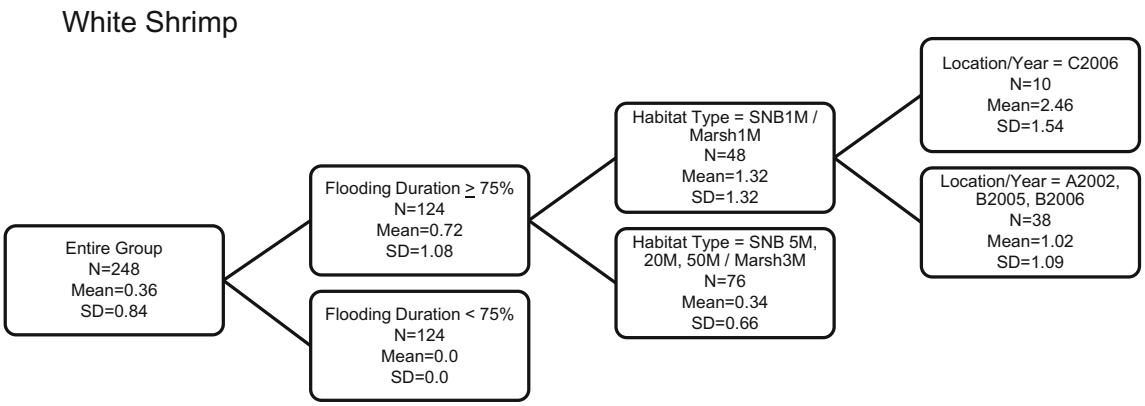

Fig. 7 Regression tree showing distribution of white shrimp in the study area. Each split in the tree includes the name of the explanatory variable, number of cases (*N*), mean log transformed density (number per square meter), and the standard deviation (*SD*). The cumulative R^2 for the whole model is 0.44

mean salinities±SE for SNB1M, SNB5M, and SNB20M were 26.1±0.13, 26.0±0.15, and 26.1±0.13, respectively; mean DOs± SE (mg l^{-1}) were 5.1±0.13, 5.0±0.16, and 4.7±0.12, respectively.

We recovered most experimental shrimp at SNB sites when the experiment was terminated (Fig. 9). No significant difference in recovery rates was apparent among habitat types (ANOVA: MS=0.025, $F_{2,20}$=2.438, P=0.116).

Although no difference in shrimp growth rates was detected among the SNB habitat types using the metric TL (ANOVA: MS=0.140, $F_{2,20}$=1.863, P=0.184), this comparison was significant using biomass as the metric (ANOVA: MS=1814.25, $F_{2,20}$=3.489, P=0.040). Mean growth rates (mg day^{-1}) were lower in SNB1M than SNB5M, but similar between SNB20M and both SNB1M and SNB5M (Fig. 10). Based on linear regression analysis that included data from all nonvegetated mesocosms, growth rates were marginally related to flooding duration (percentage of time mesocosm sites were flooded; P<0.052, R^2=0.19), an indication that low-water events negatively affected the growth of shrimp confined within those mesocosms placed at relatively high elevation intertidal sites. We considered growth rates in mesocosms with flooding durations <94 % (three SNB1M mesocosms) to be artifacts of the experimental method, and after excluding the data from these mesocosms, this relationship between growth and flooding duration was not significant (P=0.702). Excluding the data from the high SNB1M sites increased mean daily growth rates in this habitat type to 1.1±0.17 SE mm TL and 69.9±14.51 SE mg, and these rates are similar to the rates derived from SNB5M (1.2±0.09 SE mm TL, 88.8± 5.28 SE mg) and SNB20M (1.0±0.11 SE mm TL, 67.6±8.83 SE mg) sites (Fig. 10). No difference in growth rates among habitat types was detected after excluding the data from these high SNB1M sites (ANOVA: TL: MS=0.076, $F_{2,15}$=0.993, P=0.394; biomass: MS=897.77, $F_{2,15}$=1.931, P=0.179).

Potential predators recovered when the mesocosms were emptied included spot *Leiostomus xanthurus*, inshore

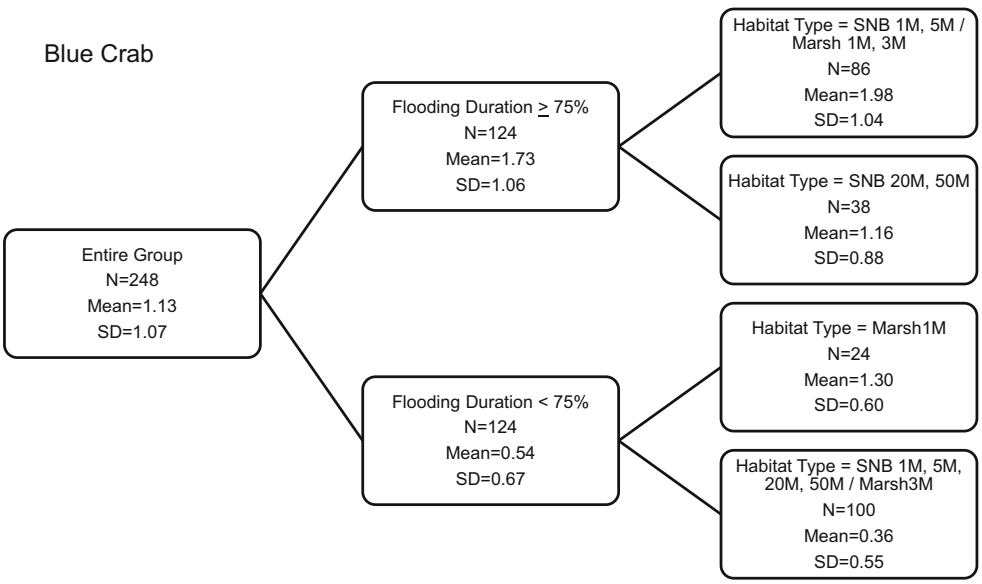

Fig. 8 Regression tree showing distribution of blue crab in the study area. Each split in the tree includes the name of the explanatory variable, number of cases (*N*), mean log-transformed density (number per square meter), and the standard deviation (*SD*). The cumulative R^2 for the whole model is 0.44

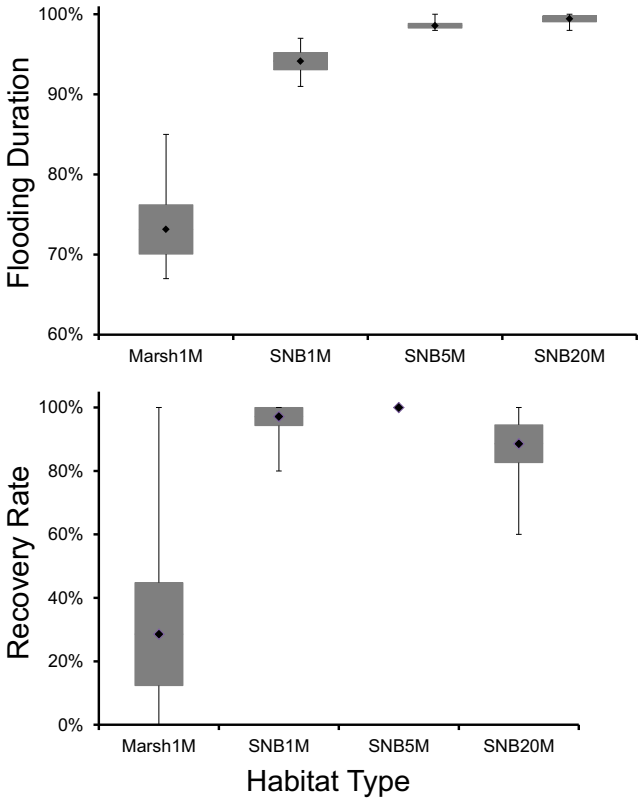

Fig. 9 Average flooding durations (*top panel*) and brown shrimp recovery rates (*bottom panel*) from growth mesocosms in different habitat types. Flooding duration was calculated as hours site inundated/total hours of experiment × 100. *Bars* show ranges, and *diamond markers* represent means. *Boxes* represent 1 SE around the means. Values were calculated from seven samples in each habitat type

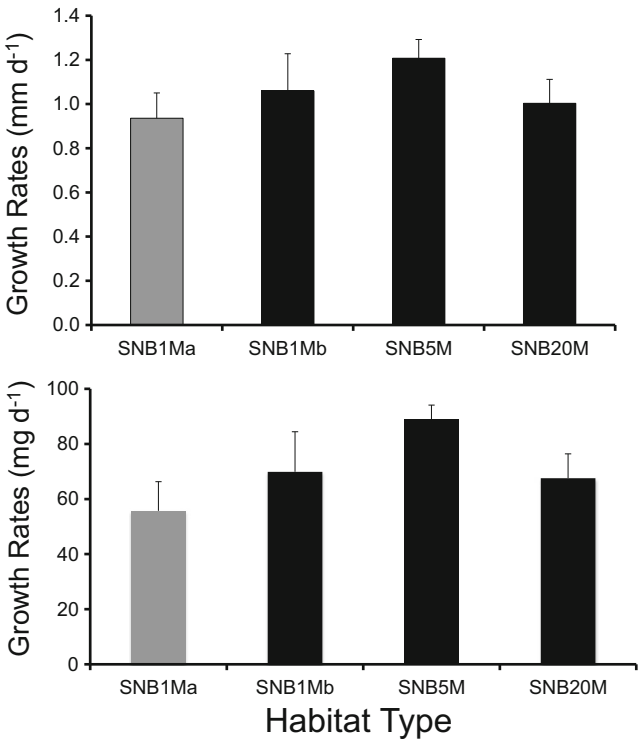

Fig. 10 Comparison of brown shrimp daily growth rates in TL (*above*) and biomass (*below*) among habitat types. Means and SEs were calculated from four samples for SNB1Mb and seven samples in each of the other habitat types. *Solid black bars* represent data with flooding durations of at least 94 % and judged unaffected by experimental artifacts

lizardfish *Synodus foetens*, speckled worm eel, star drum *Stellifer lanceolatus*, blue crab, and lesser blue crab *Callinectes similis*. No significant relationship (P=0.810) was detected in our analysis between the number of experimental shrimp and the total predator biomass recovered from the mesocosms. Unmarked penaeid shrimps and other organisms (potential competitors) also were collected when we cleared the mesocosms. These unmarked animals did not seem to affect shrimp growth rates. No significant relationships between shrimp growth and the biomass of total penaeids (P=0.564), total crustaceans (P=0.787), or total organisms (P=0.862) were detected.

Discussion

Nekton distributional patterns in Barataria Bay are similar in some ways to those in Galveston Bay. Consistent with the Galveston Bay model, the nekton assemblage is generally concentrated along the marsh shoreline. For example, densities of most species in our study were highest within 1 m of the marsh shoreline at Marsh1M and SNB1M sites. Others have documented similar patterns in Barataria Bay (Rakocinski et al. 1992; Baltz et al. 1993), Galveston Bay (Rozas and Zimmerman 2000; Minello and Rozas 2002; Minello et al. 2008), and other estuaries of the north central Gulf of Mexico (Peterson and Turner 1994; Minello 1999; Rakocinski and McCall 2005; Shervette and Gelwick 2008).

Our study, however, also revealed clear departures from the Galveston Bay model, and differences were twofold. The vegetated marsh edge (Marsh1M) in Barataria Bay did not contain the highest densities of brown shrimp, blue crab, and white shrimp when these species were most abundant in the estuary as predicted by the Galveston Bay model (Minello and Rozas 2002; Minello et al. 2008). Although highest densities occurred near the marsh edge, spring brown shrimp densities were higher in SNB1M than Marsh1M, and no statistical differences were detected in fall densities of blue crab or white shrimp between these two habitat types. Further, densities of some species in Barataria Bay dropped off much more steeply with distance into the marsh than documented for Galveston Bay (Reed et al. 2007). For example, brown shrimp (spring) and white shrimp (fall) densities in Barataria Bay declined between Marsh1M and Marsh3M by 91 and 92 %, whereas the Galveston Bay model predicts a decline of only 56 and 46 %, respectively (Minello et al. 2008).

In Barataria Bay, interior marsh (Marsh3M and landward) appeared to be used relatively less, and SNB relatively more,

as habitat for brown shrimp, white shrimp, and blue crab than the Galveston Bay model would predict. A possible explanation for reduced use of marsh edge and interior in Barataria Bay is that the elevation of the marsh surface may be higher and the slopes of these marshes may be steeper, and therefore, marsh surfaces may be inundated less and be less available than those in Galveston Bay. High marshes, which have a relatively short flooding duration, contain lower densities of fishery species than low marshes (Rozas and Reed 1993; Rozas and Zimmerman 2000). In our study, shrimp density at marsh edge sites was positively related to the flooding duration of this habitat type. Minello et al. (2012) reported a shorter mean flooding duration for saltmarsh in Barataria Bay than Galveston Bay. This result, however, was based on a single location from each estuary and must be considered tentative until additional sites within each estuary can be investigated, given the likelihood that variation in flooding duration within estuaries is high. Differences in marsh slope could also be important, as the total area of useable habitat for nekton is constrained by marsh slope; with any given water level, as marsh slope increases, the area of inundated marsh decreases. The spatial distribution of nekton also may be related to their overall density. Nekton may be compelled to move into less favorable habitat only after some threshold density is reached at the marsh edge, which presumably is the preferred habitat type. For example, blue crab and brown shrimp in Barataria Bay appeared to select marsh edge during seasons when their abundance was relatively low. When they were most abundant in the estuary, however, densities of blue crab (fall) and brown shrimp (spring) in marsh edge were similar or lower than those in some of the other habitat types. The regression tree models for brown shrimp and blue crab clearly indicated these seasonal shifts in habitat use. Shifts in habitat use also may be responses to seasonal changes in prey availability (Orth and van Montfrans 1990; Whaley and Minello 2002; Davis et al. 2014) or ontogenetic changes in food or refuge requirements (Thomas et al. 1990).

Fry (2008) arrived at a similar conclusion about the use of SNB by brown shrimp and estimated that most (67 %) of the brown shrimp production from the Louisiana delta was derived from estuarine bays rather than marshes. He based this conclusion on the presence of resident, small (mean=46–47 mm TL) juvenile brown shrimp in bay waters, the identification of bay habitat as the origin of most shrimp production as indicated by $\delta^{34}S$ isotope tags, and the high (5:1) bay/marsh area ratio in Barataria Bay. Others, however, have proposed a stronger link between fishery production and estuarine wetlands based on correlative relationships between the amount of marsh or marsh edge and fishery landings (Turner 1997; Faller 1979; Browder et al. 1989), experimental studies of marsh value (Zimmerman et al 2000), and ecological models (Haas et al. 2004; Roth et al. 2008). Fry (2008) surmised that marshes could be more important than his data indicate if most of bay production is derived from SNB near marshes and little is from deep water remote from estuarine marshes. Our data support such a distribution pattern with densities of small juvenile brown shrimp and other species being higher over SNB near the marsh than at deeper sites up to 50 m away. These nearshore SNB areas, however, would not increase brown shrimp production by enhancing growth based on our growth experiment. As these individuals increase in size, they move into deeper water farther from the marsh shore (Baltz et al. 1993; Jones et al. 2002), but information about brown shrimp from deep water is limited. Quantitative nekton density data from these deep parts of the estuary are difficult to collect (Rozas and Minello 1997), and information on growth and survival even more so, but such data would be useful for estimating the contribution of deep water habitats to overall estuarine production. Even so, scaling up from these patterns of small-scale distribution and habitat-specific vital rates in estuaries to population-level effects in coastal waters is complex (Levin 1992; Rose 2000; Sullivan et al. 2000).

Fishes represented a less important component of nekton than decapod crustaceans in our study, and their density patterns were less clearly defined. Perhaps, this taxonomic group would have been more prominent in our study had we sampled additional habitat types (e.g., small ponds, tidal creeks) or during different parts of the tidal cycle. Rakocinski et al. (1992) and Baltz et al. (1993) examined habitat use by marsh-edge fishes using drop samples collected in marsh vegetation and over SNB within 18 m of the marsh shoreline. Their five most abundant species (naked goby, gulf menhaden, darter goby, bay anchovy, and speckled worm eel) were also abundant in our study. As in our study, gulf menhaden and bay anchovy appeared to avoid marsh vegetation, but unlike our study, darter goby and silver perch were clearly associated with marsh vegetation in their study (Rakocinski et al. 1992; Baltz et al. 1993).

The combined data from 3 years and three locations in Barataria Bay appeared to represent general nekton distribution patterns in spring and fall for the dominant species examined. However, distributions among habitat types varied over locations/years for some species, most notably brown shrimp and blue crab in the fall. This interaction for brown shrimp appeared to be due to samples collected at location C in 2006, where no shrimp were collected in SNB1M and the highest mean density occurred at SNB5M. Marsh flooding before this sampling period was relatively low (54 %) and may have affected habitat selection, as indicated by the regression tree analysis. Fall blue crab distributions among habitats also varied with location/year, and the overall pattern for this species suggested little differentiation among habitats near the marsh and a negative selection only against SNB20M and SNB50M. Location/year differences also were apparent for other species, where few individuals were collected in one or two locations; habitat-specific density patterns in these situations were more

difficult to discern. For example, the close association of purple marsh crab with vegetated marsh edge was most clearly apparent where this species was abundant (location A in spring and location C in fall). Speckled worm eel did not occur at location A, but its affinity for SNB was clear from density patterns observed at the other two locations.

The mesocosms used in our growth experiment were designed to hold water over short periods of low tide allowing for measurements of growth as if the intertidal habitat was continually flooded. However, extended periods of low water during the experiment and poor shrimp recovery rates related to flooding duration near mesocosms indicated that low growth in high elevation mesocosms was an artifact of the experimental method. We considered our estimates of brown shrimp growth rates reliable after discarding the data from the mesocosms that possibly failed to hold water during extended low-water events. These estimates (1.0–1.2 mm TL day^{-1}, 68–89 mg day^{-1}) were similar among the SNB habitat types in our study and comparable to values reported from other experiments conducted in SNB (Minello and Zimmerman 1991; Fry et al. 2003; Rozas and Minello 2009, 2011).

Our experiments allowed us to obtain growth rates that should be representative of the specific SNB habitat types we included in our study if mesocosm effects were minimal. We took several precautions, in addition to discarding unreliable data from mesocosms suspected of draining, to minimize possible experimental artifacts (Rozas and Minello 2009). We used a stocking density similar to natural densities of brown shrimp in the study area. The spatial layout of habitat treatments was randomized, and each habitat treatment was replicated seven times. We limited the duration of the experiment to 7 days to reduce the possibility of depleting benthic prey (infauna) and causing excessive fouling on mesocosm walls or increasing sedimentation within the mesocosms. Three ports in the walls of each mesocosm allowed water exchange and equilibration of internal and external conditions except during low water. The ports also may have allowed entry of potential planktonic prey. We minimized the time between capture of experimental shrimp and their transfer into the mesocosms to limit stress on these organisms. The similarity in our growth estimates to those of free ranging populations (St. Amant et al. 1966; Knudsen et al. 1977) and the high survival rates in all of the SNB mesocosms give us confidence that other experimental artifacts were minimal.

Growth rates are often assumed to be more rapid for shrimp using the vegetated marsh surface than those using SNB, but this assumption has not been adequately tested (Minello et al. 2003). Experimental data that would test this assumption have been limited, as in our study, by the difficulty of maintaining an aquatic environment in this intertidal habitat during low tide events. Realistic estimates of growth in intertidal habitats including tidal marsh are essential, and a search for the means to measure growth rates in these habitats should be a priority.

Our study provides habitat-specific density data for important fishery species and abundant estuarine residents from Barataria Bay as well as habitat-specific growth rates for brown shrimp in SNB. Distributional patterns of nekton among habitats differ from the patterns predicted by the Galveston Bay model, suggesting that in Barataria Bay, shallow nonvegetated bottom may be relatively more important as habitat than previously assumed. Brown shrimp growth rates did not differ among nonvegetated habitat types and were comparable to those reported from other studies conducted in similar habitat. Additional experimental approaches are needed to estimate habitat-related growth and mortality in this system before we make conclusions about relative habitat value. The differences in nekton spatial distributions between Barataria Bay and Galveston Bay revealed by our study underscore a critical need to understand the processes that generate these patterns.

Acknowledgments This research was conducted through the NOAA Fisheries Service Southeast Fisheries Science Center by personnel from the Fishery Ecology Branch (FEB) located at the Galveston Laboratory and the Estuarine Habitats and Coastal Fisheries Center in Lafayette, Louisiana. The assistance of everyone in the FEB was essential for the successful completion of this project. In particular, we thank Jason Breeding, Harley Clinton, Molly Dillender, Jim Ditty, Jennifer Doerr, Chris Fontenot, John Foret, Engi Guy, Ebony Henderson, Shawn Hillen, Joni Kernan, Kirk Kilfoyle, Mark London, Carolyn Martin, Joy Merino, Suraida Nañez-James, Cherie O'Brien, Lori Ortega, Matt Prine, Brian Riley, Juan Salas, Bubba Taylor, Katie Turner, and Elizabeth Wilson for helping to collect and process samples. Philip Caldwell produced Fig. 1. University of New Orleans students John Anderson, Danny Bond, and Sarah Fearnley also helped collect nekton samples. Ken Able provided review comments that improved the original manuscript. We thank Denise Reed for the help in securing support for nekton sampling in Area A. The Port of Fourchon (Ted Falgout, Executive Director) kindly provided access to location C. We acknowledge the Louisiana Coastal Wetlands Conservation and Restoration Task Force, NOAA Restoration Center, and NOAA Fisheries Service Southeast Fisheries Science Center for funding this research project. The findings and conclusions in this report are those of the authors and do not necessarily represent the views of the NOAA Fisheries Service.

References

Anonymous. 1958. Symposium on the classification of brackish waters. *Oikos* 9: 311–312.

Baker, R., B. Fry, L.P. Rozas, and T.J. Minello. 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. *Marine Ecology Progress Series* 490: 37–52.

Baker, R., M. Fujiwara, and T.J. Minello. 2014. Juvenile growth and mortality effects on white shrimp *Litopenaeus setiferus* population dynamics in the northern Gulf of Mexico. *Fisheries Research* 155: 74–82.

Baltz, D.M., C. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* 36: 109–126.

Baumann, R.R. 1987. Physical variables, p. 8–17. In W. H. Conner and J. W. Day, Jr. (eds.), The ecology of Barataria Basin, Louisiana—An

estuarine profile. US Fish and Wildlife Service Biology Report 85(7.13), Washington, DC

Beck, M.W., K.L. Heck Jr., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641.

Browder, J.A., L.N. May Jr., A. Rosenthal, J.G. Gosselink, and R.H. Bauman. 1989. Modeling future trends in wetland loss and brown shrimp production in Louisiana using thematic mapper imagery. *Remote Sensing of Environment* 28: 45–59.

Byrne, P.A., M. Borengasser, G. Drew, R.A. Muller, L. Smith Jr., and C. Wax. 1976. *Barataria basin: Hydrologic and climatology processes*. Baton Rouge, Louisiana: Center for Wetland Resources, Louisiana State University, Sea Grant Publication No. LSU-T-76-010. 176.

Chabreck, R.H. 1972. *Vegetation, water, and soil characteristics of the Louisiana coastal region. Agriculture Experiment Station Bulletin No. 664*. Baton Rouge, Louisiana: Louisiana State University. 72 p.

Chesney, E.J., D.M. Baltz, and R.G. Thomas. 2000. Louisiana estuarine and coastal fisheries and habitats: Perspectives from a fish's eye view. *Ecological Applications* 10: 350–366.

CPRA. 2012. *Louisiana's comprehensive master plan for a sustainable coast*. Baton Rouge, LA: Coastal Protection and Restoration Authority of Louisiana. 189 p.

Davis, B., C. Mattone, and M. Sheaves. 2014. Bottom–up control regulates patterns of fish connectivity and assemblage structure in coastal wetlands. *Marine Ecology Progress Series* 500: 175–186.

Day Jr., J.W., G.P. Shaffer, L.D. Britsch, D.J. Reed, S.R. Hawes, and D. Cahoon. 2000. Pattern and process of land loss in the Mississippi Delta: A spatial and temporal analysis of wetland habitat change. *Estuaries* 23: 425–438.

Deáth, G. 2002. Multivariate regression trees: A new technique for modeling species–environment relationships. *Ecology* 83: 1105–1117.

Faller, K.H. 1979. Shoreline as a controlling factor in commercial shrimp production. NASA Technical Memorandum 72-732, 33 p.

Fry, B. 2008. Open bays as nurseries for Louisiana brown shrimp. *Estuaries and Coasts* 31: 776–789.

Fry, B., D. Baltz, M. Benfield, J. Fleeger, A. Gace, H.A. Haas, and Z. Quinones. 2003. Chemical indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. *Estuaries* 26: 82–97.

Gunter, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. In *Estuaries. AAAS, Pub. No. 83*, ed. G.H. Lauff, 621–638. DC: Washington.

Haas, H.L., K.A. Rose, B. Fry, T.J. Minello, and L.P. Rozas. 2004. Brown shrimp on the edge: Linking habitat to survival using an individual-based simulation model. *Ecological Applications* 14: 1232–1247.

Jones, R.F., D.M. Baltz, and R.L. Allen. 2002. Patterns of resource use by fishes and macroinvertebrates in Barataria Bay, Louisiana. *Marine Ecology Progress Series* 237: 271–289.

Knudsen, E.E., W.H. Herke, and J.M. Mackler. 1977. The growth rate of marked juvenile brown shrimp, *Penaeus aztecus*, in a semi-impounded Louisiana coastal marsh. *Proceedings of the Gulf Caribbean Fisheries Institute* 29: 144–159.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Linscombe, G. and R. Chabreck. 2001. 2001 Louisiana coastal marsh-vegetative type map. Louisiana Department of Wildlife and Fisheries, Fur and Refuge Division, and the US Geological Survey National Wetlands Research Center. http://brownmarsh.net/data/III_7.htm.

Mace, M.M. III and L.P. Rozas. 2015. Estimating natural mortality rates of juvenile white shrimp *Litopenaeus setiferus*. *Estuaries and Coasts* (in press). DOI 10.1007/s12237-014-9901-7).

Mendelssohn, I.A., G.L. Anderson, D.M. Baltz, R. Caffey, K.R. Carman, J.W. Fleeger, S.B. Joye, Q. Lin, E. Maltby, E.B. Overton, and L.P. Rozas. 2012. Oil impacts to coastal wetlands: implications for the Mississippi River Delta ecosystem after the Deepwater Horizon oil spill. *BioScience* 62: 562–574.

Milliken, G.A., and D.E. Johnson. 1992. *Analysis of messy data. Volume 1: Designed experiments*. London: Chapman and Hall. 473.

Minello, T.J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. In: Benaka L. (ed) Fish habitat: essential fish habitat and habitat rehabilitation. American Fisheries Society Symposium 22:43–75.

Minello, T.J., and L.P. Rozas. 2002. Nekton in Gulf coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12: 441–455.

Minello, T.J., and R.J. Zimmerman. 1991. The role of estuarine habitats in regulating growth and survival of juvenile penaeid shrimp. In *Frontiers in shrimp research*, ed. P. DeLoach, W.J. Dougherty, and M.A. Davidson, 1–16. Amsterdam: Elsevier Science Publishers.

Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: Testing hypotheses on density, growth, and survival through meta-analysis. *Marine Ecology Progress Series* 246: 39–59.

Minello, T.J., G.A. Matthews, P. Caldwell, and L.P. Rozas. 2008. Population and production estimates for decapod crustaceans in wetlands of Galveston Bay, Texas. *Transactions of the American Fisheries Society* 137: 129–146.

Minello, T.J., L.P. Rozas, and R. Baker. 2012. Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. *Estuaries and Coasts* 35: 501–514.

Orth, R.J., and J. van Montfrans. 1990. Utilization of marsh and seagrass bottom habitats by early stages of *Callinectes sapidus*: A latitudinal perspective. *Bulletin of Marine Science* 46: 126–144.

Perez-Farfante, I. and B. Kensley. 1997. Penaeoid and sergestoid shrimps and prawns of the world: Keys and diagnoses for the families and genera. Mémoires du Muséum National d'Historie Naturelle, Tome 175, Paris, France.

Peterson, G.W., and R.E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17: 235–262.

Quinn, G.P., and M.J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Rakocinski, C.F., and D.D. McCall. 2005. Early blue crab recruitment to alternative nursery habitats in Mississippi, USA. *Journal of Shellfish Research* 24: 253–259.

Rakocinski, C.F., D.M. Baltz, and J.W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* 80: 135–148.

Reed, D.R., A. Bell, L. Martinez, T.J. Minello, A.M.U. O'Connell, L.P. Rozas, S. Penland, R.C. Cashner, and A.M. Commagere. 2007. Modeling relationships between the abundance of fishery species, coastal wetland landscapes, and salinity in the Barataria Basin, Louisiana. Final report to NOAA National Marine Fisheries Service and Louisiana Coastal Wetlands Conservation and Restoration Task Force. University of New Orleans, New Orleans, Louisiana. 148 p

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.

Roberts, H.H. 1997. Dynamic changes of the Holocene Mississippi River delta plain: The delta cycle. *Journal of Coastal Research* 13: 605–627.

Rose, K.A. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications* 10: 367–385.

Roth, B.M., K.A. Rose, L.P. Rozas, and T.J. Minello. 2008. Relative influence of habitat fragmentation and inundation on brown shrimp

Farfantepenaeus aztecus production in northern Gulf of Mexico salt marshes. *Marine Ecology Progress Series* 359: 185–202.

Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18: 579–590.

Rozas, L.P., and T.J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20: 199–213.

Rozas, L.P., and T.J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science* 63: 481–501.

Rozas, L.P., and T.J. Minello. 2009. Using nekton growth as a metric for assessing habitat restoration by marsh terracing. *Marine Ecology Progress Series* 394: 179–193.

Rozas, L.P., and T.J. Minello. 2011. Variation in penaeid shrimp growth rates along an estuarine salinity gradient: Implications for managing river diversions. *Journal of Experimental Marine Biology and Ecology* 397: 196–207.

Rozas, L.P., and D.J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Marine Ecology Progress Series* 96: 147–157.

Rozas, L.P., and R.J. Zimmerman. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). *Marine Ecology Progress Series* 193: 217–239.

Rozas, L.P., T.J. Minello, and D.D. Dantin. 2012. Use of shallow lagoon habitats by nekton of the northeastern Gulf of Mexico. *Estuaries and Coasts* 35: 572–586.

Rozas, L.P., Minello, T.J., and M.S. Miles. 2014. Effect of Deepwater Horizon oil on growth rates of juvenile penaeid shrimps. *Estuaries and Coasts* 37: 1403–1414.

Shervette, V.R., and F. Gelwick. 2008. Relative nursery function of oyster, vegetated marsh edge, and nonvegetated bottom habitats for juvenile white shrimp *Litopenaeus setiferus*. *Wetlands Ecology and Management* 16: 405–419.

St. Amant, L.S., J.G. Broom, and T.B. Ford. 1966. Studies of the brown shrimp, *Penaeus aztecus*, in Barataria Bay, Louisiana, 1962–1965. *Proceedings of the Gulf Caribbean Fisheries Institute* 18: 1–17.

Stunz, G., T.J. Minello, and P.S. Levin. 2002. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. *Estuaries* 25: 76–85.

Sullivan, M.C., R.K. Cowen, K.W. Able, and M.P. Fahay. 2000. Spatial scaling of recruitment in four continental self fisheries. *Marine Ecology Progress Series* 207: 141–154.

Thomas, J.L., R.J. Zimmerman, and T.J. Minello. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bulletin of Marine Science* 46: 115–125.

Turner, R.E. 1997. Wetland loss in the northern Gulf of Mexico: Multiple working hypotheses. *Estuaries* 20: 1–13.

Viosca Jr., P. 1928. Louisiana wet lands and the value of their wild life and fishery resources. *Ecology* 9: 216–229.

Visser, J.M., C.E. Sasser, R.H. Chabreck, and R.G. Linscombe. 1998. Marsh vegetation types of the Mississippi River Deltaic Plain. *Estuaries* 21: 818–828.

Whaley, S.D., and T.J. Minello. 2002. The distribution of benthic infauna of a Texas salt marsh in relation to the marsh edge. *Wetlands* 22: 753–766.

Whitehead, A., Dubansky, B., Bodinier, C., Garcia, T.I., Miles, S., Pilley, C., Raghunathan, V., Roach, J.L., Walker, N., Walter, R.B., Rice, C.D., and Galvez, F. 2011. Genomic and physiological footprint of the Deepwater Horizon oil spill on resident marsh fishes. *PNAS Early Edition* (www.pnas.org/cgi/doi/10.1073/pnas.1109545108).

Yoklavich, M., Blackhart, K., Brown, S.K. Greene C., Minello, T., Noji, T., Parke, M., Parrish, F., Smith, K., Stone, R., and Wakefield, W.W. 2010. Marine fisheries habitat assessment improvement plan. Report of the National Marine Fisheries Service habitat assessment improvement plan team. NOAA Technical Memorandum NMFS-F/SPO-108, 115 p.

Zimmerman, R.J., T.J. Minello, and G. Zamora Jr. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fishery Bulletin* 82: 325–336.

Zimmerman R.J., T.J. Minello, and L.P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In *Concepts and controversies in tidal marsh ecology*, eds. Weinstein M.P. and D.A. Kreeger, 293–314. Dordrecht: Kluwer Academic Publishers.